

AN ANNOTATED, ANALYTICAL BIBLIOGRAPHY OF "MONSTROUS" CICINDELINAE BEETLES, AND SOME PROBLEMS THEY AWAKEN¹

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ABSTRACT: Brief introduction is given to monstrous beetles, with comment on the value of their exact analysis. All published accounts of such tiger beetles found (1849 - present) are cited, annotated, and their anomalies indexed. The 42 individuals recorded include 13 with branched appendages; of the 10 analyzable, only one (leg triplication) was sufficiently well presented to permit determination of secondary symmetries. It conforms to "Bateson's rules". Those specimens are listed for which re-analysis is desirable, along with problems some awaken.

At first thought, it seems astonishing that about 73% of some 690 natural occurrences of "monstrous" beetles having malformed, branched appendages known to Balazuc (1947) should be representatives of but four of the 140 or more families of beetles. The four are: Carabidae, including Cicindelinae, (ca. 42%), Scarabaeidae *s.l.* plus Lucanidae (ca. 16%), and Cerambycidae (ca. 15%). However, it is likely that the responsible causal developmental mishaps, or (the less likely) regenerative responses to injury, befall all kinds of beetles with fairly similar frequencies. The pronounced bias reflected by members of the four families probably owes chiefly to their being favorites among collectors, hence they are especially sought, collected, kept in large series, and closely examined by many for notable variations.

Cicindelinae, too, are much admired, fervently collected, and even enjoy the distinction of a journal devoted solely to their kind. It therefore seems surprising that tiger beetles have provided comparatively few published records of individuals with abnormal branching appendages (compared with the Carabinae, for example). Perhaps the hyperactive adults of so many tiger beetle species lead to speedy culling of monstrous adult forms from their populations. If so, those collected present but a fraction of the frequency of those in the population that entered adult life with branched appendages.

I have had cause to search for published, analytical accounts of cicindelids with branched appendages in connection with a study (in MS) of a specimen of *Cicindela scutellaris lecontei* (Hald.). This female has a trifurcated left antenna as well as a branched left mandible; all else seems normal. No cicindelid appears to have been recorded with a similarly

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anomalous mandible. Indeed duplications of mandibles are among the rarest of anomalies reported among beetles; only 8 cases of possible or actual mandibular furcation have been described or mentioned. That apparent rarity may owe to the facts that mandibles are essential to predation and feeding, and are structural units, whereas other appendages ordinarily have 2 or more parts (palps) and as many as 11 (antennae), or rarely more. Hence other appendages have from a few to many more elements that potentially may give rise to branches. None, when branched, is so likely to be as great a threat to life as is a non-functional mandible.

I have searched for published cases of monstrous cicindelids by scanning titles in Derksen and Scheidung-Göllner (1963 - 1968, references from 1864 through 1900) and Zoological Record (from 1900 to June 1990), as well as references in Bateson (1894) and Balazuc (1947, 1969). Regrettably the titles of a large majority of reports on monstrous beetles give no clue to the taxa treated. As the total potentially relevant publications on monstrous beetles exceeds 1000, I was unable to review a majority of them. Accordingly I obtained and scanned or read articles by well-known workers on cicindelids whether or not their titles seemed promising (e.g., those of Walther Horn), those explicitly indicating a cicindelid anomaly, and those longer works dealing with a variety of teratological cases. Occasionally the latter provided a relevant case (e.g., Mocquerys 1860; Cockayne 1938).

There is very likely a fair number of described anomalies of tiger beetles, the obscure references to which are unknown to me. I give below an annotated listing of the accounts of all cicindelid anomalies I have found and read (other than the numerous accounts of peculiar maculations, and trivial reports of mismatched and incompletely expanded or matured elytra). It is hoped that items known to others, but missing from the annotated list and index, will be brought to my attention or published in *Cicindela* so that ultimately there will be available a complete bibliography, or nearly so, of teratological tiger beetles.

The importance of detailed accounts, supplemented by reliable illustrations, especially of duplicated and reduplicated appendages and their parts is that they provide information, and some boundary conditions, of the naturally occurring outcomes of developmental errors and processes. Currently workers in molecular biology are making very considerable advances in the possible explanation of developmental duplications by experiments (mostly in chick, mouse and salamanders), by biochemical analyses, and by *ad hoc* theory (e.g. see: Meinert in Kay and Smith 1989; Brockes 1990; Noji *et al.* 1991; Wanek *et al.* 1991). The theoretical interpretations of course must prove adequate to explain what is found in nature if they are to be widely applicable. It must be emphasized that many

naturally occurring cases on record far exceed in complexity the duplications so far produced by experimentation.

Bateson (1894) made a very thorough morphological study of duplicate and reduplicate anomalies of appendages in both vertebrates and invertebrates. He defined as "*primary symmetries*" those shown by corresponding appendages from the two sides of a bilateral organism; e.g., the arms of a man, or the 2 prothoracic legs of an insect, which are related to one-another as symmetrical mirror-images. To coleopterists, among his notable contributions was the demonstration that, as with many other kinds of organisms, only a minority of *carefully* analysed cases among beetles with branched appendages fail to show "*secondary symmetries*". For example: if a leg of a beetle bears an extra femur and tarsus, and the orientations of the morphologically dorsal, ventral, anterior and posterior surfaces of each element of the leg has been determined, then the duplicated parts are almost always found to exhibit secondary symmetries; that is, they are mirror-images (but not necessarily dimensionally so) of the corresponding parts of the leg from which they arise, and therefore are similar to those parts of the corresponding leg on the opposite side of the body. He also showed that reduplicated (trifurcated) appendages are fairly common anomalies, and that in them all three of the branches tend to lie in the same plane when each element is fully extended along its main axis. In trifurcations, the parts of the middle member are mirror-images of the corresponding parts of both the limb from which it and its system member arose, as well as of those of its sister branch. If the asymmetrical letter F is used to denote the symmetry of antennal parts, and the parts of the branches of an antenna be indicated as 0 (the original length) from which the sister branches 1 and 2 arise together, then the case just described may be represented as: $F_{0,1}\bar{F}, F_{2,}$ or $F_{2,1}\bar{F}, F_0$ (depending on the orientation of the primary length of branch 0).

Genuine exceptions to these rules have been found, but they are too few to have given rise to alternative or additional "rules". They may possibly form a sizable, but lesser class, for there are now very large numbers (1000 or more) of published, relevant cases among insects, which are unresolvable pro or con because the original descriptions and their illustrations are inadequate for a decisive analysis of their morphology. Regrettably this is also so for all but one of the relatively small number of described duplicate and reduplicate appendages of tiger beetles. It is desirable that henceforth adequate analyses and illustrations be required for all descriptions of teratologies. If the original specimens on which accounts were based are still available for study, careful analysis of most of them is to be desired. Some cases may defy resolution because of inadequate morphological landmarks, but they too should be

thoroughly analyzed so that this may be known to be so (as Bateson and Cockayne have so carefully done for certain cases). Means for drawing up suitable descriptions are given by Bateson (1894) and Balazuc (1947); Cockayne's notes and analyses (1925-1938, 1943) on specimens of monstrous beetles may serve as easily available, useful models.

Annotated bibliography of "monstrous" cicindelids.

Specific names and their authors are those given in the texts. Other than Horn's (1938) recording of an artefactual chimaera, references are limited to those describing naturally occurring developmental, regulatory, or possibly regenerative errors that occurred in stages prior to completion of pupation. Structures apart from those discussed are said or assumed to be normal. Simple deformations caused by mechanical damage to the pupa or still teneral adult, as described by Antoine (1913), are omitted. Horn (1927) has stated under what circumstances departures from the normal range of maculation are worthy of record, and he supplied nearly 40 examples he judged to be such; no other references to peculiarities of markings are cited, nor do the common occurrences of unduly shortened or mismatched elytral lengths since Shelford (1915) and Horn (1927) provide sufficient records. The bibliography is arranged in chronological order; most of the individual cases of anomalies are numbered.

Guérin-Méneville, F.E. 1849. Cicindéletes de la Guinée Portugaise, découvertes par M. Bocandé, avec des notes de ce voyageur et la description des espèces nouvelles. *Rev. mag. Zool.* (2 serie) 1: 76-84, 138-150.

1. *C. anthracina* (p. 82), ♂: L(ef)t mesoleg developmentally atrophied; consists of coxa, trochanter, and a small rounded stump of femur.

Mocquerys, S. 1860. *Recueil de coléoptères anormaux*. No. 4, 16 printed pp (not numbered), ill. Published by author; Rouen. [Republished by la Société des Amis des Science naturelles de Rouen, with an introduction by J. Bourgeois: 1880. *Coléoptères anormaux* par Feu M. S. Mocquerys, Rouen;., xvi + 142 pp, 125 figs.]

2. *Cicindela campestris* (Fab.) (1860, 9th unnumbered page with fig.; 1880 reference, p. 88, fig.; here species attributed to "Lin." by editor), ♂ (sexed from figure): R(ight) antenna 7 articles, with a spherical tubercle at the anterior apices of articles 4-6, and apically on 7.

Gadeau de Kerville, H. 1886. [Cinque coléoptères du genre mélomélie]. *Ann. Soc. ent. France* (ser. 6) 6, *Bull. Séances*: CLXXIX.

3. *C. decemguttata* Fabr. v. *durvillei* Dej., ♂: R antenna slightly longer than L; article-8 doubled, with the anterior branch having normal articles 9-11, posterior branch with 2 articles together equal in length to normal articles 9-11. Horn's (1908, p 19) citation is erroneous.
- Gadeau de Kerville, H. 1888. Coléoptères et hémiptères anormaux. *ibid.* 8, Bull. Séances: LXXXII-LXXXIV.
4. *Cicindela sylvatica* L., ♀: R antenna slightly shorter than L; article-3 bifurcate, bearing the remainder of the primary antenna and supplementary article. Bateson (1894, p 550) saw the specimen and classed it as either "partially amorphous or mutilated". Horn's (1908, p 19) citation is erroneous.
- Smith, J.D. 1888. An abnormal *Cicindela*. Proc. Entomol. Soc. Wash. 1:107.
5. *Cicindela belfragei*, ? sex: a sharp tubercle on left side of "thorax".
- Lopez, C. 1891. A proposito di alcune Coleotteri anormale. Riv. ital. Sci. nat. e Boll. Naturalista, Siena. 11: 22-26.
6. *Cicindela sylvicola* Dejean, ? sex: L antenna bifurcate at 8th article; anterior branch but a single article; posterior branch with 3 normal articles.
7. *Cicindela sylvatica* L., ? sex: ? R or L antenna (analogous to Mocquerys' specimen, see #2 above): with 7 articles, and with 4 spherical tubercles as described by Mocquerys; antenna shortened beyond 3rd article; article-4 very short, bent on self, concave above, and much swollen. Both of Lopez' specimens are listed by Cockayne (1938, p 392) as among those beetles with furcate antennae of which the symmetry "...is not clear". It is doubtful that Mocquerys' specimen of *C. campestris* and Lopez' of *C. sylvatica* have furcate antenna. I concur that the symmetry relations (if any) of both cases 2 and 7 are unclear; the specimens need restudy.
- Balbi, E. 1897. Difformitates et monstrositates coleopterorum. Naturalista Siciliano 2: 150-159, 2 pls.
8. *Cicindela campestris* L., p 152, figs 1 and 1(@2x), ? sex: L mandible with a long, slender, gently inwardly curved, pointed prolongation, arising laterally near midlength, which is white, with pearly reflections (a failure to tan and color normally like the remainder of the mandible?).
9. *Cicindela campestris* L., p 152, figs 2 and 2(@2x), ? sex: R and L antenna 11-jointed, of normal lengths but with deformed articles. R antenna has articles 1-4 distinct, article-5 as long as the first 4 to-

gether, remaining articles shortened. L antenna has the 1st article as long as normal segments 1-5 joined; remaining articles shortened. fig. 1(@2x) and text in part difficult to reconcile.

Horn, W. 1905. Systematischer Index der Cicindeliden. Deutsche Entomol. Ztschr 1905; Beilage, 56 pp.

10. *Therates rugifer* Horn, holotype, p 11, ♀: a valid species, but rugulose sculpturing of head and prothorax "...in typo monstrosa!" [Horn 1902. Neue Cicindeliden gesammelt von Fruhstorfer in Tonkin 1900. Deutsche Entomol. Ztschr. 1902: 65-75 --- also mentions a marked deepening of the juxta-sutural engraving of the elytra, a blister on left elytron.] See also comments on pp 475-476, and fig. 36, in Horn 1927 (below).

Moore, R. 1906. Notes on the habits of *Cicindela*. Entomol. News 17: 338-343.

11. *Cicindela purpurea*, ? sex: ankylosis of the elytra.

Codina, A. 1908. Noticia sobre una monstruositat que's trova en el palpe esquerra d'una female *Cicindela paludosa* var. *sabulicola* Waltl. Institut. Catalana d'Hist. Nat. 5: 74-76, 1 fig.

12. *Cicindela paludosa* var. *sabulicola* Waltl., ♀: L antenna trifurcate, article-6 shortened, apically widened, 7th still wider apically, with 2 articular facets, from the inner of which extends 4 normal articles completing the apex of the normal (original) antenna; a bifurcate, "U"-shaped article-8, attaches to the outer facet of 7; from each limb of 8 there extends a length of 3 articles; each accessory limb shorter than normal, the outermost shortest.

Köster, W. 1910. Monströse Fühlerbildung. Entomol. Blätt. Biol. System. Käfer. 6: 245.

13. *Cicindela germanica* L. abb. *coerulea* Hrbst, ♀: L antenna with only 5 regular articles present; a 4-article limb given off below from the apically 2-facetted article-3, terminal article of 2nd limb is bowed dorsally.

Shelford, V. 1915. Abnormalities and regeneration in *Cicindela*. Ann. Entomol. Soc. Amer. 8: 291-295, pl. 24.

14. *Cicindela tranquebarica*, fig. 1, ? sex: deformed labrum.
 14a. *Cicindela tranquebarica*, Fig. 5, ? sex: R elytron shorter.
 15. *Cicindela sexguttata*, fig. 4, ? sex: L elytron shorter.

- Campos, F. 1918. Algunos casos teratologicos observados en los Artropodos. *Ann. Ent. Soc. Amer.* 11: 97-98.
16. *Tetracha suturalis* Horn, ? sex: L middle leg with apparently 6-jointed tarsus; perhaps derived by a fracture and healing of article-3.
- Luigioni, P. 1926. Coleotteri anomali. Sopre due casi di polimelia riscontrati in due individui di "*Cicindela germanica*" Lin. *Pontifica Acad. Sci., Rome, Atti* 79: 81-86, 2 figs.
17. *Cicindela germanica* Lin., 1 fig., ? sex: R fore tibia with 3 tarsi of 5 articles each; apex of tibia angulate, spatulate posteriorly beyond normal apex. The normal tarsus arises from the not-angulate apex, the 2 accessory tarsi from the broadened angulation.
- *18. *Cicindela germanica* Lin., 1 fig., ? sex: L mid-leg trifurcate, all from same coxa; the anterior 2 sister legs, each with its own trochanter, arise as though from a bifurcated base; both smaller than normal, anterior the larger; posterior leg normal. All appear to have arisen in same plane. The middle leg is the mirror image of both the anterior and posterior (normal) legs --- case conforms to Bateson's rules.
- Horn, W. 1927. Ueber "Monstrositäten" and verwandte Vorgänge bei Cicindelinen, Teil I. II. Wanderversammlung Deutscher Entomologen in Stettin. *Entomolog. Mitt.* 16: 471-477, 48 figs. [No additional parts appear to have been published.]
19. *C. aurulenta* subsp. *setosomalaris* Horn, fig. and case 34, ? sex: antenna (? side) of 4 articles, article-4 strongly flattened, distally broadened, bisinuate apically. [Horn also gives 3 cases of abnormal antennae (doubtfully natural) in two *Pogonostoma coeruleum* G. Lap. and one *P. chalybeum* Klug but he comments that these may be due to deformations caused in packing somewhat teneral individuals; see cases and figures 52-54.]
20. *Tricondyla cyanea* subsp. *brunnea* Dokht., fig. and case 33, ? sex: anterior rim of pronotum deeply, slightly asymmetrically, marginate — appearing as 2 separate, prominent lobes.
21. *Collyris levigata* Horn, fig. and case 49, ? sex: shortened and strongly, transversely crimped pronotum.
22. *C. campestris* L., fig. and case 51, ♀: foretarsus (? side) strongly shortened, 4 articles, 3rd bifurcate, with a reduced claw-bearing segment arising from lateral fork of article-3.
23. *C. japana* Mtsch., fig. and case 1, ? sex: L elytron shortened. There are other cases in other species of R or L elytra shortened, ? sexes: see figs. 11, R; 14, L; 16, R; 17, R; 18, R; 22, L; 39, L.
24. *C. striolata* Ill., fig. and case 2, ? sex: both elytra symmetrically shortened.

- Cockayne, E.A. 1938. Supernumerary antennae in insects. Trans. Roy. Entomol. Soc. London. 87: 385-396, 1 pl.
25. *Cicindela 10-guttata* Fabr., p 391, figs. 4, 4A, ? sex: R antenna normal for first six segments; seventh has two joints at distal end; from the outer arises a branch with four segments a little shorter than normal, otherwise well-formed; from the inner arises another branch of four segments. The first of these very broad, short, thick; the second also shorter, thicker than a normal ninth segment, so this may be a fused double structure. [The words are Cockayne's, but the description has been abbreviated. He classified the specimen as having "Antennae with two extra parts, the symmetry of which is not clear" (p 390).]
- Horn, W. 1938. 2000 Zeichnungen von Cicindelinae. Entomol. Beihefte, Berlin-Dahlem 5: 71 pp, 90 pls.
C. dohrni Dokht., p 11. The holotype has been lost. Very probably an artefact; pronotum and elytra are from *C. macrocnema obliquans* Chaud.; head from a common type with dense, short setation of the genae and above. (Not included in numerical sequence because specimen probably a hoax.)
- Wood, G.R. 1965. A trifurcate tiger beetle antenna (Coleoptera: Cicindelidae). Jour. Kansas Entomol. Soc. 38: 392-394, 2 figs.
26. *Cicindela scutellaris lecontei* (Hald.); ? sex: R antenna trifurcate at apically V-shaped article-9; from each limb of 9 extends a branch of 2 articles; a single, incompletely divided article extends between the arms of the V. All 3 branches appear to lie in the horizontal plane; the anterior of these terminated the "normal" portion of the antenna.
- Willis, H.L. 1967. Bionomics and zoogeography of tiger beetles of saline habitats in the central United States (Coleoptera: Cicindelidae). Univ. Kansas Sci. Bull. 47: 145-313, 168 figs.
27. *Cicindela nevadica knausi*, p 205, figs 85, 86, ♂: L antenna incompletely trifurcated; partially bifurcate at apical fourth of article-3, hence with 2 apical articular facets bearing (? above) a limb of 8 individual articles, and (? below) a longer limb in which articles-7 and -8 of that limb are incompletely marked off, and doubled, but not separated lengthwise. In this respect, the antenna differs from most trifurcate antennae in which the 2 accessory branches arise from a common element — see cases 12, 26, and those in Bateson (1894), Balazuc (1947, 1969), and Cockayne (1938).
[Willis 1969. Unusual antennal deformity in *Cicindela nevadica*. *Cicindela* 1: 1, and cover photo, again touches on this specimen.]
28. *C. nevadica knausi*, p 205, fig. 82, ♂: labrum deformed, L side.

29. *C. nevadica nevadica*, p 205, fig. 81, ♂: labrum deformed, L side.
 30. *Cicindela nevadica knausi*, p 205, Fig. 84, ♀: 4 holes, from small to very large, in R elytron; 30a. — another minor case in subspecies *olmosa* (p 205, fig. 83, female: R elytron).

Larochelle, A. 1974. Unusual antennal deformity in *Cicindela punctulata* Olivier. *Cicindela* 6: 69-70, 1 fig.

31. *Cicindela punctulata* Olivier, ♂: L antenna presumably with representation of only 10 articles; article-6 bifurcate posteriorly in basal half, but without any attached, segmented ramus.

Summary and Index of Anomalies

The annotated citations give access to reported natural occurrences of structurally anomalous cicindelids. Represented are 23 species, and 6 genera of which 18 are species of *Cicindela*. In all, there are some 42 individual cases among the 31 numbered listings.

Representing each case by its number in the list, its sex (where stated), the side involved (when given), and by placing that set of 3 ordered items in parentheses if falling in more than one category of anomaly [as examples: 1 ♂ L; 5 ? L; 22 ♀ ?; and (13 ♀ L)]; all of the individuals may be categorized as follows.

A. Branched or multiple appendages (*Schizomelics*)

1. antenna bifurcate: 3 ♂ R; 6 ? L; (13 ♀ L); 31 ♂ L.
2. antennae trifurcate: 4 ♀ L; 12 ♀ L; 25 ? R; 26 ? R; 27 ♂ L.
3. mandible: 8 ? L (a neomorph?).
4. legs triplicate: 18 ? L.
5. tarsi duplicate: (22 ♀ ?).
6. tarsi triplicate: 17 ? R.

B. Malformations

7. antenna: 2 ♂ R; 7 ? ?; 9 ? R + 9 ? L; (13 ♀ L); 19 ? ?.
8. labrum: 14 ? RL; 28 ♂ L; 29 ♂ L.
9. pronotum: 5 ? L; 20 ? -; 21 ? -.
10. elytron short: 14a ? R; 15 ? L; 23 ? L [+ 7 cases listed under 23, of which 4R, 3L and ? sex for all].
11. elytra, both short: 24 ? -.
12. elytra ankylosed: 11 ? -.
13. elytra with holes: 30 ♀ R; 30a ♀ R.
14. leg: 1 ♂ L.
15. tarsus, extra joint: 16 ? L.
16. tarsus missing joint: (22 ♀ ?).
17. sculpture: 10 ♀ -.

COMMENTARY

None of the above categories is unique to cicindelids; see Balazuc (1947, 1969) for many examples among other beetles.

Of the 13 cases of abnormally branched and multiple appendages, the description and illustration of only one (# 18) permits a decision regarding the symmetry relations among its parts. They are, in anterior to posterior order, $F_2, 1\bar{F}, F_0$, hence in accord with Bateson's rules (see p 3).

If available for restudy, cases 3, 6, 12, 26 and 27 (antennae) deserve careful analysis of the symmetries of their branches. Case 27 is of special importance, for it possesses two points of incipient branching, namely at articles -3 and -9 of the probably original antenna; two such widely separated branch points are remarkable. It is important that the secondary symmetries (if any) be determined and placed on record. Cases 4 and 25 have been declared unresolvable as mentioned in the annotations, and this is probably so for case 13 as well.

The supernumerary tarsi of case 17 should offer no difficulty for a determination of their symmetries; that of case 22 is very likely to prove unanalyzable.

Cases 2 and 7 deserve restudy on their own merits, and also because Cockayne (1938) placed case 2 on his list of beetles with *furcated* antennae. The "spherical tubercles" present at the apical ends of the terminal four articles may in fact prove to represent aborted remnants of the 4 missing articles of the 2 aberrant antennae; or perhaps they can be proven to be true branches (unlikely, however, for the small terminal tubercle). No anomalous branching of an order higher than trifurcation, involving at most 2 branch points from the original axis is known to me for appendages of insects. In any case, these anomalies complicate the problem of antennal development in the pupal beetle.

Finally, Balbi's extraordinary specimens (cases 8 and 9) could profitably be restudied; the mandible is apparently but uncertainly anomalous in ways that none of the small number of known furcate mandibles are. Furthermore, the apparent maintenance of normal antennal lengths by differential shortening when a single (but different) joint in each antenna is exceptionally long awakens a puzzling problem in regulation during differentiation.

The summaries for cases of schizomely and malformation, and the two taken collectively, show no statistical tendency for the right or left side to be affected more frequently.

It is hoped that in future the sex of a specimen having a structural anomaly will always be given. Of the forty specimens mentioned in the annotations, only 14 are of stated sex (7 $\sigma\sigma$, 7 ♀♀). It is not likely that most anomalies fall unequally upon the two sexes but, if any do, how can it become known unless the sexes of all specimens, or nearly all, are stated?

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- _____. 1938. Supernumerary antennae in insects. Trans. Entomol. Soc. London 87:385-396, 1 pl.
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*Prof. Pinto received the following information from Dr. Marco Bologna, of the Università degli Studi dell'Aquila, who, for his own needs had already searched for the Balbi collection. It is not at the museum in Genoa, where Balbi lived, nor has it been traced to any other Italian museum. It is presumed destroyed.